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ORTHOGENESIS AS OBSERVED FROM PALE- ONTOLOGICAL EVIDENCE BEGINNING IN THE YEAR 1889¹

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1. THE ORIGIN OF SPECIES

THE Origin of Species is now clearly understood in the hard parts of invertebrates and of vertebrates, and there is little to be added as to the *modes of mechanical evolution*. No chances or experiments are tried by Nature. The process is continuous, adaptive, mechanically perfect in every Mutation of Waagen. As shown in actual observations by all close students of vertebrate and invertebrate morphology during the last fifty-two years, and as summed up in the remarkable contribution of D'Arcy Wentworth Thompson (1917) on "Growth and Form," animal mechanisms compete with each other in close analogy to humanly made machines—automobiles, typewriters, aeroplanes. Consequently, while Nature is constantly standardizing her machines through individual competition and producing flocks of birds and shoals of fishes which are so precisely alike that animals of the same age, sex, environment and heredity *show no perceptible variation*, she is also frequently substituting more perfect and more adaptable machines and discarding older and less adaptable ones, exactly as man is doing in the case of his automobiles, his typewriters, and his aeroplanes. Thus the naturalist and the paleontolog-

¹ Illustrated by twelve lantern slides exhibiting mutations of *Ammonites*, of *Spirifer*, of *Paludina*; rectigradations of the grinding teeth of lemuroid Primates; evolution of proportion from the rhynchocephalian type of *Hatteria* to the dinosaurs and birds of the genera *Deinodon*, *Struthiomimus*, and *Diatryma*.

ist are alike impressed with the incessant action of Natural Selection on animal mechanisms and with the new testimonials to this aspect of Darwin's great principle.

When it comes to the *origins* either of new characters or of new proportions quite different is the attitude of observers of mechanical evolution; no evidence whatever has been forthcoming from the same fifty-two years of close observation and research as to the *causes* of origin, at the same time the *modes* of origin of all mechanical characters are indubitably orthogenetic.

To further clarify the bearing of palæontology on orthogenesis, I desire to point out that all visible mechanical evolution goes hand in hand with invisible physicochemical evolution; and that there are steps in evolution which are primarily physical, others which are primarily chemical, others which are primarily mechanical. Therefore the experimental botanist, zoologist, biochemist, biophysicist, or geneticist, has the opportunity to win immortal fame by discovering the causes of mechanical evolution.

Meanwhile the palæontologist enjoys the entirely unique position of being the only competent observer of the Origin of Species so far as specific characters are recorded in the hard parts of animals and the relatively few soft parts which are preserved in a fossil condition.

2. ORTHOGENETIC ORIGIN OF NEW CHARACTERS

All agree that sound induction either as to the origin of new characters or their transformation is an exceedingly difficult matter. It has taken me thirty-three years of uninterrupted observation in many groups of mammals and reptiles to reach the conclusion that the origin of new characters is invariably orthogenetic.

In 1889 I first observed (Osborn, 1889.46) that new cusps originate on the grinding teeth of Eocene Primates, now recognized as lemuroids, in a definite and adaptive manner from minute shadowy beginnings which are mechanically adjusted to similar minute shadowy

beginnings of opposing cusps in the other jaw; whereby there evolves a continuous reciprocal mechanism not dissimilar to the reciprocal services of the Yale key and the Yale lock. The evolution of the key below proceeds with the evolution of the lock above. The process does not go very far in the Primates, but in the purely herbivorous ungulates, like the horse and the elephant, the reciprocal grinding mechanism reaches a degree of complexity to which the most intricate lock and key devised by man present but a feeble parallel. Every mechanical device in the upper grinding teeth, adapted to the fine comminution of grasses, is *reversed* in the lower grinding teeth, on the principle of mechanical action and reaction; nowhere in nature is reciprocal mechanical co-adaptation more perfectly evolved than in the upper and lower grinding teeth of mammals.

Between 1889 (Osborn, 1890.47) and 1891 (Osborn, 1891.53) I made what I now believe to be an *unsound induction* from this evidence that this continuous mechanical origin tended to support the Lamarckian theory of the inheritance of adaptive reactions. I first termed the orthogenetic process "definite variation"; later I termed it "progressively adaptive variation"; by the year 1908 I realized that these new adaptively arising tooth elements were not variations in Darwin's sense at all, and I applied to them the distinctive term *rectigradations* (Osborn, 1908.314). In the meantime I abandoned the Lamarckian explanation and in 1895 (Osborn, 1895.97) I started out upon a *search for the unknown factors of evolution*, a search in which I am still busily occupied.

To return to the difficulty of making sound inductions as to the origin of new characters in hard parts, in 1889 I opened a long correspondence with the leading exponent of Darwinism in Great Britain, Edward B. Poulton, who admitted the evidence but interpreted the facts in the Darwinian way, namely, as the selection of mechanical successes from non-observed mechanical failures. It is a good thing to have a number of skeptical friends

about; it sharpens your powers of observation and makes you much more cautious about your inductions. My original observations on the Primates required corroboration, and this I have sought through the observation of the origin of new characters in many other kinds of mammals traced in their evolution over very long periods of time, especially the horses, the rhinoceroses, and recently the proboscideans, but most profoundly and exhaustively the titanotheres, an extinct family remotely related to the horses, which I have studied monographically for twenty-one years.¹

Even by trying to keep an absolutely open eye and mind, entirely uninfluenced by any theory, or preconception, or opinion, I have been unable to find a single exception among these many different kinds of mammals to the observations made on the Primates in 1888 and 1889; not a single new organ is observed to arise fortuitously or indefinitely; it always arises gradually, continuously, and adaptively from its minute shadowy beginnings. This continuous reciprocal, mechanical co-adaptation seems to be an established fact in evolution, and is established most strongly where explanation or search for causes seems to be most difficult.

I am not enthusiastic about the adoption of the term orthogenesis, admirably significant as it is in its Greek derivation, first, because Eimer connected it with Lamarck's and Buffon's principles of inheritance of acquired modifications, and, second, because it does injustice to the first great observer of direct adaptive origins in nature, namely, the German palæontologist Wilhelm Heinrich Waagen, whose observations in 1869 laid the foundation of all subsequent work both among the in-

¹ Osborn, H. F., "The Titanotheres of Ancient Wyoming, Dakota, and Nebraska. Life and Geography of the Central Rocky Mountain Region in Eocene and Oligocene Times. Evolution of the Titanotheres Family. The Causes of Development and Extinction of Mammals," *U. S. Geol. Survey Monograph No. 55*. [Unpublished.] Completed for the Survey June 30, 1920. This monograph is the most complete and exhaustive analysis that has thus far been made of the evolution of any family of organisms.

vertebrates and the vertebrates. To the best of my knowledge *he was the first naturalist to observe how new species actually arise in nature.* Compare Waagen's description (1869) of the genesis of new characters in the shells of cephalopods (*Ammonites subradiatus*) with those which Osborn (1889-1921) has observed in the teeth:

"Thus the species if considered as such may be conceived and considered as a species, but in contrast with earlier or later forms [i.e., ancestors or descendants] as a mutation. Now as regards the value of these above-defined conceptions, variety and mutation, on closer consideration a quite decided difference in value becomes apparent. The former conception [variety], in the highest degree variable, appears to be of small systematic value; while the latter [mutation], although in minute characters, is highly constant, always surely recognizable; on which account far greater weight must be put upon Mutations, they ought to be very precisely denoted and held fast to with great persistence."

Twenty years later the German palæontologist Melchior Neumayr observed this process of continuous development, generation after generation, in a certain definite direction for which he proposed the term "*Mutationsrichtung*." Thus the "mutation of Waagen" arises continuously through the inner working or tendency, the "*Mutationsrichtung*" of Neumayr.

It was not until 1894 that William B. Scott brought Waagen's term "Mutation" to the notice of vertebrate palæontologists in this country, in antithesis to Darwin's term Variation. Waagen's "Mutation" means one thing, Darwin's "Variation" means quite another, as pointed out by Scott above. The term Mutation in Waagen's sense is now widely but not universally used by palæontologists to designate intermediate gradations of minor taxonomic rank which are observed in ascending or descending series of animals to connect the larger stages of evolution which we call Species. As an ele-

mentary species a "Mutation" of Waagen is comparable to a "Mutant" of De Vries in external appearance, but not in mode of origin, because one arises through a continuous "*Mutationsrichtung*," while the other arises through accidental germinal saltation. To my mind the continuous or discontinuous mode of origin either of a "mutation" or of a "mutant" is of small account as compared with the fortuitous or orthogenetic nature of the impulse in the germplasm which gives rise to it.²

So far as I know all observers of the hard parts of extinct animals, whether vertebrate or invertebrate, confirm this classic observation of Waagen, and many in this special field of observation also confirm the "*Mutationsrichtung*" of Neumayr. So far as I personally have observed, this principle of "*Mutationsrichtung*" is especially dominant in the origins of characters; here at least other interpretations are not applicable; there is no question of Selection between two alternatives, adaptive and inadaptive, because the inadaptive does not occur, the whole process is adaptive and the difference between two organisms is the rapidity and direction with which the "*Mutationsrichtung*" is acting. This is the same in the hard parts of the molluscs *Ammonites*, *Paludina*, and *Planorbis*, as it is in the mammals *Equus*, *Rhinoceros*, and *Elephas*.

3. THE ORIGIN OF NEW PROPORTIONS

In the evolution of proportions, that is, proportions in the different parts of skeleton and skull as in *Sphenodon*, *Deinodon*, *Struthiomimus*, *Diatryma*, it appears *probable* that Selection may be constantly working on all adaptive fluctuations of proportion in connection with ontogenetic modifications in proportion which are also adaptive, as in the classic case cited by both Darwin and Lamarek of the length of the neck of the giraffe.

² F. A. Bather in 1905 (*Proc. Geol. Soc.*, Vol. 61, pp. lxxii-lxxiii) most clearly elucidated Waagen's conception of the Formenreihe and of the Mutation in *Ammonites*.

It has been demonstrated experimentally that the limb proportions in the brief life of a dog may be modified from the cursorial to the saltatorial type by amputating the fore limb. This is a process of reciprocal Modification and Selection which Osborn, Baldwin, and Morgan term Organic or Coincident Selection. I have devoted an immense amount of study to the causes of the evolution of proportion and have come to the conclusion that orthogenesis in the evolution of proportion may be apparent rather than real. In other words, whenever a character assumes a survival or elimination value, it may develop very rapidly through the selection of fluctuations in the right direction and may result in apparent but not real orthogenesis.

4. SUMMARY AS TO ORTHOGENESIS

The visible "mutation of Waagen," or "definite variation" or "rectigradation" of Osborn appears to depend on the "Mutationsrichtung" in the germ-plasm. The final question in my mind, as in yours, must be, if such a "*Mutationsrichtung*" exists, is it the "internal perfecting tendency," is it the "vitalism," is it the "creative evolution" which the majority of biologists are so skeptical about?

I observe that it is not. I observe that while the "*Mutationsrichtung*" is a real process, it differs from any kind of internal perfecting tendency in the fact that it consists in an adaptive reaction to the particular environment in which a series of organisms is placed, or to which it migrates. For example, the internal perfecting tendency to arboreal life does not manifest itself when the animal seeks an aquatic life. Conversely, aquatic adaptations are not constantly springing up among arboreal mammals. Observations on fossil forms have led to Dollo's remarkable generalization regarding "alternate adaptation," which renders any form of internal perfecting tendency in any predetermined direction inadmissible.

Summary of Observations.—In the hard parts of animals orthogenesis is observed both in the origin of new adaptive characters and in the evolution of proportions. (1) The induction as to cause may be different in the two cases. (2) In the origin of new adaptive characters orthogenesis is attributable to definite germinal tendencies. (3) The origin of changes of proportion which are subject to *modification* may be partly attributable to Organic Selection. (4) There is positive disproof of an internal perfecting tendency (Vitalism) in either the origin of new characters or the origin of proportions. (5) There are certain changes of length and breadth proportion both in the shells of invertebrates and the skulls of vertebrates which can not be explained by Organic Selection. (6) There is very strong support in fossil series for Selection incessantly acting on all characters of survival or elimination value.

The above six principles are those which I have derived from forty years of continuous observation; they are actual modes of the mechanical evolution of new species for which we have no theoretic explanation, unless it be that of Organic Selection in the single case above noted.

Summary of Opinions.—I may add as a matter of personal opinion and hypothesis three points: *first*, that we are as remote from adequate explanation of the nature and *causes of mechanical evolution* of the hard parts of animals as we were when Aristotle first speculated on this subject three hundred years B.C.; *second*, that the chief outlook for experiment is in the domain of physics; *third*, that the explanation, if ever it is to be found, is to be along the lines of four systems of energy (=Tetraplasy, Tetrakinesis, Osborn) which surround the origin and development of every character in every organism; *fourth*, I think it is possible that we may never fathom all the causes of mechanical evolution or of the origin of new mechanical characters, but shall have to remain content with observing the modes of mechanical evolution,

just as embryologists and geneticists are observing the modes of development, from the fertilized ovum to the mature individual, without in the least understanding either the cause or the nature of the process of development which goes on under their eyes every day.

In conclusion, it is the great biological achievement of the last half century that palæontologists have discovered *how* new characters and new species originate. It may be the achievement of the experimental biologists during the next half century to explain *why* new characters and new species originate.

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